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Forest Succession

Concepts and Application

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Preface

Succession—nothing in plant, community, or ecosystem ecology has been so elaborated by terminology, so much reviewed, and yet so much the center of controversy. In a general sense, every ecologist uses the concept in teaching and research, but no two ecologists seem to have a unified concept of the details of succession. The word was used by Thoreau to describe, from a naturalist's point of view, the general changes observed during the transition of an old field to a forest. As data accumulated, a lengthy taxonomy of succession developed around early twentieth century ecologists such as Cooper, Clements, and Gleason. Now, nearer the end of the century, and after much discussion concerning the nature of vegetation communities, where do ecologists stand with respect to knowledge of ecological succession?

The intent of this book is not to rehash classic philosophies of succession that have emerged through the past several decades of study, but to provide a forum for ecologists to present their current research and present-day interpretation of data. To this end, we brought together a group of scientists currently studying terrestrial plant succession, who represent research experience in a broad spectrum of different ecosystem types. The results of that meeting led to this book, which presents to the reader a unique summary of contemporary research on forest succession.

The conference* was held in June 1980 at the Mountain Lake Hotel,

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Mountain Lake, Virginia. One reason for choosing this site, along with the natural beauty of the Alleghenies, was the hope that in an isolated location with minimal outside interruption substantial synthesis of ideas about succession could occur. Before the conference, we attempted to anticipate what would be the result of bringing such a diverse array of scientists to debate a controversial topic. Would the conference become bogged in semantic debates? Would the heat of disagreements generate defensiveness and divisiveness?

This trepidation was not borne out in reality. The conference participants were deeply interested in discussing one another's data. Individuals who had different viewpoints on succession were glad to have the chance to try to understand the source(s) of these differences. Scientists who felt that their data did not match the textbook definitions of succession were able to exchange views with other scientists who held similar feelings based on different ecosystems. The excitement of having so many new and old ideas, and new and old data sets about succession, was contagious.

Prose fails to capture the mood and excitement of scientific inquiry when ecologists have the glimmer of being able to synthesize an idea as important as succession. This book provides the building blocks that may lead to such a synthesis. Even if we restrict our discussion to forests, we do not yet understand succession in as thorough a way as an introductory textbook leads one to think. The conference at Mountain Lake and this book lead us, and hopefully the reader, to feel that although we do not know everything there is to know about succession, we at least possess a body of theory and empirical data that support an increasingly refined effort of analysis and documentation.

Finally, we should point out that the conference was made successful in part by the much appreciated assistance of Tom Doyle, Carolyn Henley, Joy Simmons, Tom Smith, Roger Walker, and David Weinstein. We wish to thank Forest Stearns, David Reichle, Robert Van Hook, Stanley Auerbach, Tom Callahan, Jerry Olson, and Robert O'Neill, who gave helpful suggestions regarding organization and content of the meeting and of this volume.

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Chapter 16

Successional Studies of a Rain Forest in Mexico

Arturo Gómez-Pompa and Carlos Vázquez-Yanes

Introduction

Secondary succession, although examined in various climatic regions, has been most intensively studied in the north temperate zone. The motivation for these studies has been scientific interest in the investigation of vegetational changes through time and space, and not because secondary succession in these areas represents the best expression of changes during the regeneration of terrestrial ecosystems.

In comparison, succession in the hot, humid tropics is more pronounced, occurs in a shorter period of time, and apparently lacks noticeable changes during the year, primarily as a result of the favorable climate. Although the stages of tropical succession are well defined, the number of successional studies in the tropics are few. Representative examples include: Budowski (1961); Kellman (1969, 1970); Symington (1933); Wyatt-Smith (1955); Webb et al. (1972); Opler et al. (1977); Snedaker (1970); Harcombe (1972); Ewel (1971); Blum (1968); and the studies in Mexico, which will be cited in this chapter. Due to the lack of tropical studies, a large part of successional theory is not based on information from the ecological region most favorable for the expression of the successional process.

This simple, but important fact has caused considerable confusion in our understanding of the temporal changes in terrestrial ecosystems following disturbance. In the temperate zone, the length of winter drastically affects the behavior of plant and animal species, resulting in a successional development composed of a series of annually interrupted events. While the process of temperate succession is fascinating, this annual interruption has obscured our understanding of the continuous population changes that occur in a given locality through time after disturbance.

Our studies of rain forest regeneration in the hot, humid tropics of Mexico (Gomez-Pompa et al. 1976) have resulted in the construction of a simple, graphic model, which we feel explains more completely the general process of plant succession in a site. The model is based primarily on the life cycles and survival of individual species in time and space. Figure 16.1 illustrates this model, and presents plant life cycle patterns along a successional time gradient.

This model accounts for all the possible ways that a species could exist in an active form (excluding seeds and other propagules) in a given moment. Also included are the presence and behavior of certain species that are dominants at different successional times. For each case and place, the number and frequency of distinct types of species that are dominants at different successional times. For each case and place, the number and frequency of distinct types of species may vary, but species with well-defined life cycles will always be present in each successional stage. Thus, for example, the first stages of succession will always contain some short-lived species, and a successional stage of 4–5 years will have some long-lived trees present. According to the scheme presented here, some areas may lack specific life cycles or stages. Such is the case in some hot, humid savannas, where small trees or shrubs dominate through long periods of time, even though long-lived trees are predicted through succession. Succession in these areas is arrested by the lack of arboreal germ plasm (Gomez-Pompa et al. 1972). The model allows us to study any site. Use of the floristic composition and life cycles of the species present permits evaluation and prediction of future changes in the vegetation, assuming that environmental conditions do not vary greatly.

This model is incomplete, since it does not include animals or microorganisms, which play important roles in succession. However, these two groups are subordinate to the primary producers. Thus, though incomplete, the model provides a clear idea of vegetational changes through succession. On the other hand, it should be noted that our knowledge of animal population changes and life cycles through secondary succession is rather rudimentary. The same could be said about successional changes in the microbial flora and saprophytes. Clearly, lack of information about these two components of the changing ecosystem restricts our complete understanding of plant life cycles. The presence or absence of a plant species may depend on the presence or absence of certain animals that are dispersers, disseminators and predators, or on microorganisms that may inhibit or stimulate plant growth.

The complexity and nature of succession varies according to the type of ecosystem examined. For this reason it has been impossible, so far, to develop a general model of regeneration that can be applied to all ecosys-

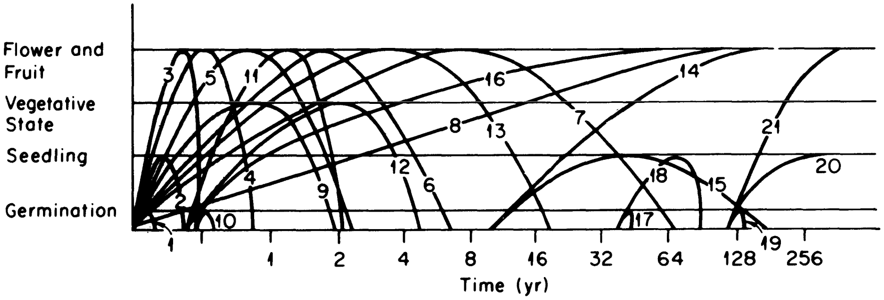


Figure 16.1. A model of life cycle patterns along a time gradient in the successional process. Each one represents a complete or an incomplete life cycle. (1) Species that germinate and die. (2) Species that germinate, produce a few leaves, and die. (3) Species that complete their life cycle in a few months. (4) Annual species. (5) Biennial species. (6) Species with a life cycle of only a few years (less than 10). (7) Species with a long life span, several decades, but eventually dying (species from old secondary forests). (8) Primary species with life spans of hundreds of years that have lived since the beginning of the succession. (9) Species that never reach the stage of sexual reproduction. (10) Species that germinate a few months after the succession begins and soon die. (11) Annual species that germinate after the succession begins. (12) Species that germinate after the succession begins but do not reach the stage of sexual reproduction. (13) Species with a short life cycles (less than 30 years). (14) Species with long life cycle that germinate when succession is well advanced. (15) Species that germinate when the succession is stage for a few years. (16) Species that germinate a few months after succession begins and then have a life cycle hundreds of years long (primary species). (17) Species that germinate and die in old successional stages. (18) Species that germinate and live at the seedling or young plant stage in old successional stages, and then die. (19) Species that germinate and die in the primary forest. (20) Species that germinate and grow to a seedling or "young" plant stage inside the primary forest and remain there, waiting for suitable conditions for continuing growth. (21) Species that germinate and grow in the primary rain forest and may reach the reproductive stage after having long life cycles (primary species). (Taken from Gomez-Pompa and Vazquez-Yanes 1974.)

tems. For example, in extreme environmental conditions with low species diversity, such as in arid regions, regeneration is a simplified process, which consists of the replacement of the disturbed community by another composed of the original species. On the other hand, in the humid tropics, with its diversity of species, ecosystems, and structures, regeneration is complicated. Through time, many diverse, intermediate successional stages occur before the original ecosystem is reestablished.

Regeneration in a Tropical Forest

Rain forests can be disturbed for numerous reasons. Sometimes the changes caused by the disturbance are severe, such as the massive death of the dominant tree strata when the rain forest is cleared for agriculture.

Less severe changes might include the destruction of the herbaceous strata by herbivory. Between these extremes exists a range of activities that disrupt the ecosystem and cause a series of distinct species responses.

The types of disturbance experienced by the primary tropical forest are: lightning, fires, vulcanism, tree falls caused by strong winds or animals (elephants), mortality or loss of vigor of trees resulting from disease, chemical pollutants, herbicides, arborcides, logging to extract forest products, conversion to agriculture or pasture, slash-burn agriculture, floods, and earthquakes.

The effects of forest disturbance vary widely, depending on the severity of the disturbance, the history and size of the area disturbed, and the environmental conditions during the disturbance. The sum of these initial factors, coupled with the available flora of the region, can determine the course of the first stages of regeneration. The series of species that appear through succession depends not only on external factors, but also on intrinsic species characteristics such as the length of the growing cycle, photosynthetic efficiency, and other physiological properties. From this point of view, regeneration in the hot, humid tropics can be thought of as a series of environmental changes through time. In the graphic model shown in Fig. 16.1, time represents an environment. Based on this model, it is possible to predict the existence of patterns of species establishment during a specific ecological succession.

There exist marked differences in the morphology and physiology of early successional species versus those of later seral stages of the primary forest. These differences have been observed and documented by various authors (Richards 1952; Budowski 1965). By studying the life cycles of primary and secondary species, within the context of a species distribution model through time, succession can be viewed as an autecological process and, at the same time, regeneration understood in ways outside the traditional realm of synecology. In addition, this approach permits an analysis of the direct relationships between particular species and their environments. These relations can be examined in two different ways: the first would be to study species adaptations to the environmental conditions of the particular successional stage in which they establish themselves, while the second focus would be to study environmental evolution during succession and its effect on the species of a community. Species interactions during succession play an important role in understanding this process, but their investigation has been extremely challenging, since it is very difficult to achieve a holistic approach to the problem. Nevertheless, this is a very promising area of study from the scientific viewpoint.

As Gleason and Cook (1927, p. 27–33) mentioned in their study of Puerto Rico:

> It may be repeated that plant associations are the basic units of vegetation, that they are the result of immigration and environmental selection, and their duration is short or long, depending on the rate of environmental change . . . .

> Each area of ground in which a particular complex of environmental conditions is repeated tends to be occupied by the same groups of species.

Each type of disturbance produces characteristic changes in the biotic and abiotic environments. These changes influence the floristic composition at the onset of recovery, and thereby affect later changes. Thus, for example, a very severe disturbance that eliminates practically all plant propagules in the soil will result in a long and less predictable succession. On the other hand, a small clearing in the rain forest will result in rapid, predictable changes.

Rain forests throughout the world, when disturbed, whether by a tree falling, a small fire, or the opening of a clearing for cultivation, experience a series of rapid changes. These include the ‘‘arrival’’ of a group of species that are adapted to the ecological conditions caused by the disturbance. With time, these species, which Corner (1932) has termed ‘‘weed trees,’’ promote the regeneration of the original ecosystem. Generally, this is the process of regeneration or cicatrization (so named by some authors) of the rain forest. This phenomenon has been described, in general terms, on several continents. Pioneer cicatricial species, especially the trees, that characterize the regeneration of disturbed rain forest are similar in physiognomy, physiology, and behavior. Notable examples are the genera *Cecropia* (Blum 1968; Vazquez-Yanes 1979; Schulz 1960) in tropical America, *Musanga* (Lebrum and Gilbert 1954; Aubreville 1947) in Africa, and *Macaranga* (Kartawinata 1977; Kochummen 1966; Whitmore 1975) in Asia.

Cicatrization of the Rain Forest

Floristic dominance changes with time. The first strong change occurs between the first months (characterized by the dominance of short lived herbaceous species) and first two years (according to the climatic zone). The species with short life cycles (Fig. 16.1) eventually disappear, and the vegetation (floristic dominance) changes, resulting in a temporarily stable shrub stage. The next stage is dominated by small trees. Later these species are replaced by larger trees, which dominate the upper story previously occupied by the small trees. This process (Fig. 16.1) has been documented for many tropical areas (Whitmore 1975; Halle et al. 1978). The similarity of the biological forms that dominate different stages, as well as the similarity of many species from related geographical or biogeographical zones, is remarkable.

Five stages in the regeneration of high evergreen rain forests in Mexico have been identified. The first stage is dominated by short ephemeral-lived (weeks or months) species, such as herbs. This stage can last for months and may also contain shrub or woody pioneer seedlings.

However, if the area is used as a pasture, it can remain in an arrested successional stage. The second stage is dominated by secondary shrubs that eliminate the herbs via shading. During this stage, shade species, which require lower temperatures and light levels for germination, may appear. This second stage, depending on the area, may last from 6 to 18 months. It is a period of rapid growth, dominated by short-lived shrubs (*Piper*, *Myriocarpa*, *Urera*, *Solanum*) from 1.5 to 3 m in height. In the shade produced by these shrubs some herbs from the previous stage persist, as well as new species with different ecological requirements. The third stage, which can last from 3 to 10 years, is dominated by secondary trees of low height stature (*Heliocarpus*, *Trema*, *Hampea*, *Miconia*), yet also contains taller secondary trees. These latter species, with heights of 10 m or more (*Cecropia*, *Didymopanax*, *Ochroma*, *Robinsonella*) characterize the next successional stage, which lasts from 10 to 40 years or more. Some primary trees, which ultimately reach heights of 25 m or more, also occur in this stage. These trees comprise the dominant vegetation in the fifth successional stage.

In reality, the process described above is a complex, continuous process, which is difficult to subdivide precisely. Actually, as presented in Fig. 16.1, the process is seen as a continuum through time, which can be characterized at any discrete moment by the type of life cycle of the dominant species.

Vegetation changes through time have traditionally been studied by measuring changes in one site through time and also by sampling neighboring sites with different aged vegetation. Different studies indicate that both these approaches have their limitations: the amount of time required (in the case of Method 1), and spatial variation and uncertainty concerning the original causes of disturbance in the various sites (in the case of Method 2).

Interestingly, the first studies in Mexico on secondary succession were oriented toward obtaining information on a species of enormous economic interest, *Dioscorea composita*, which is a raw material used to produce steroids. It was precisely to learn more about the behavior of this species, which acts typically like both a secondary and primary species, that led us to explore the process of ecosystem regeneration after disturbance in greater depth (Gomez-Pompa and Vasquez-Yanes 1974).

The enormous quantity of information on secondary succession in the tropics is difficult to interpret. The complexity of the process is overwhelming. The occurrence of this phenomenon in nature is readily observed, but difficult to describe with any desirable level of precision. The only thing that seems certain is that the species that appear in a particular stage possess common characteristics. This leads to two totally opposing conclusions. On the one hand, it is practically impossibile to make predictions about an ecofloristic process and difficult to identify indicator species for the different stages (Sousa 1964). On the other hand, there are certain repetitive characteristics, not only for the samples from Mexico, but from other parts of the world, both in the floristic composition and the physiognomy of the species present through succession.

Our first studies generated questions that required another type of investigation. Consequently, the strategy of our subsequent studies included investigations that could be conducted in a relatively short time, analyzing the regeneration process from several aspects (Gomez-Pompa and Vazquez-Yanes 1974). In planning these studies, we started with a very simple, graphic model (Fig. 16.2) for the process of ecosystem regeneration and regeneration triggering after a severe disturbance to the original rain forest. Using this model, we can ordinate our data to answer some of the important questions that arose when analyzing samples from different secondary successional areas. It was decided to study only one region in order to generate a large amount of information on one zone. Eventually, the study could be repeated and broadened to include other ecological zones in the same hot, humid tropical region. In the devised model, the process of regeneration through time culminates with the cicatrization or regeneration of an altered ecosystem.

The graphic model identifies various levels of investigation. One of the first objectives was to understand the causes of disturbance, and the floral and faunal composition of different successional stages in distinct ecological zones. This first level could be classified as the description of regeneration. However, an investigation at this level is insufficient for making generalizations to describe or predict regeneration patterns. We therefore decided to proceed to another level of investigation, which would help us understand the biological phenomenon that affect the presence of a species in time and space and studied patterns of individual behavior. Our investigations were oriented to regeneration of the high rain forest (Gomez-Pompa et al. 1976).

Studies on ecosystem recovery in the tropics have concentrated on areas abandoned after cultivation (old-field succession). Few studies exist on regeneration inside the rain forest. Below we present some data on both types of succession.

The development of vegetation, whether in natural clearings, cut areas, or abandoned fields, can have diverse origins. Vegetative growth from tree stumps, rhizomes, and other surviving vegetative structures can play an important role in vegetation regeneration. In certain cases, particularly in small clearings, seedlings of species removed by disturbance can be quite important.

The rate at which vacant land is covered by sun-loving, rapidly growing species, which are generally scarce or absent from the primary vegetation, suggests that plant development from seeds is a principal mechanism of vegetation regeneration, particularly in abandoned fields. Much has been said about the origin of the seeds of early colonizers. Supposedly, because of the intensity of seed predation in the tropical rain forest, few

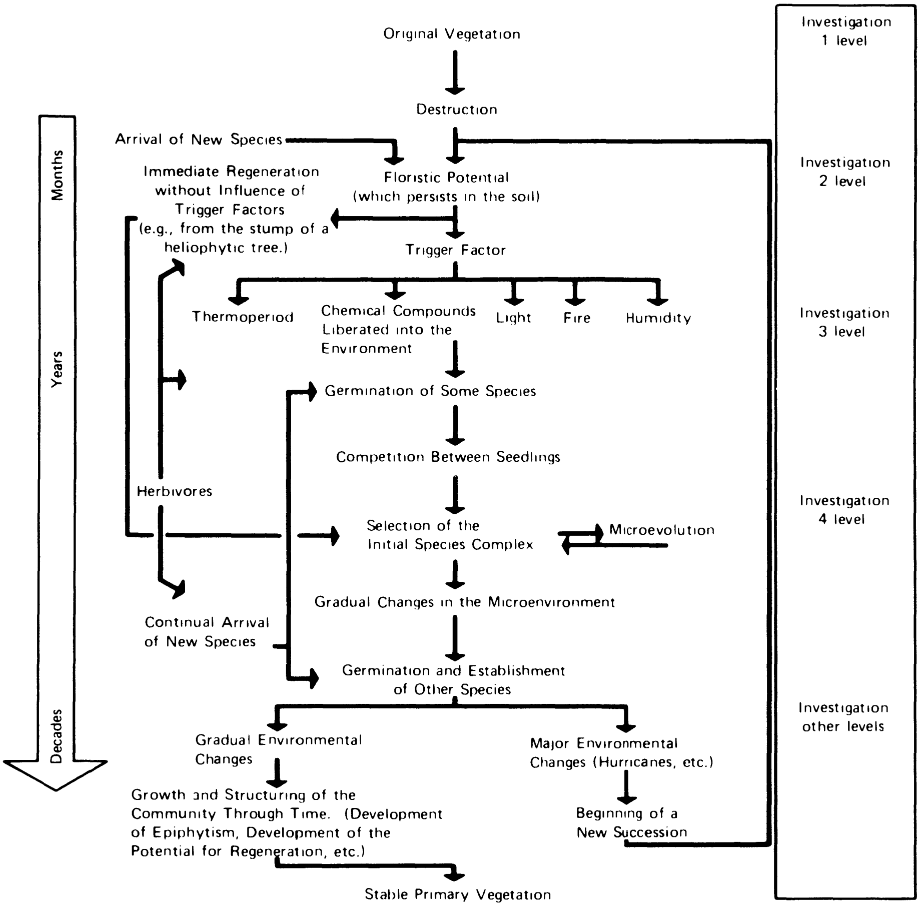


Figure 16.2. A model of research levels during succession.

seeds can survive in the soil. Therefore, colonization must occur by seeds that arrive in the disturbed area from outside. However, the presence of a great number of seeds in the rain forest soil and dormancy studies on seeds of pioneer species appear to refute the above hypothesis. This suggests that a large number of the individuals that colonize denuded soil come from seeds already present in that soil.

Few studies have examined the viable seed content of tropical rain forest soils; among the most important are Symington (1933), Liew (1973), and Ashton (1978) in Malaysia, Keay (1960) in Nigeria, Guevara and Gomez-Pompa (1972) in Mexico, and Blum (1968) in Panama. All these studies arrived at a similar conclusion: the most abundant seeds in the soil are from herbs and sun-loving, rapidly growing tree species, characteristic of large rain forest clearings or early successional stages on devegetated land. Seeds of the majority of mature rain forest species are part of the seed bank only for brief periods of time, during which they tend to germinate or are very rapidly eaten (Table 16.1).

Available data indicate that animal-dispersed pioneer species have long fruiting seasons, frequently lasting all year, and can be dispersed by very diverse species of birds and mammals. Trejo (1976) presented a list of bird species that had in their digestive tracts seeds of pioneer species common in the Los Tuxtlas region. He examined 167 birds of 37 different species and found seeds of *Cecropia obtusifolia and Trema mircrantha.* The digestive tracts of 27 of 97 birds (19 different species) contained seeds of *Cecropia*, and 49 of 122 birds (24 different species) contained seeds of *Trema.* Six bird species had seeds of both species of trees in their digestive tracts.

Wind-dispersed species, on the other hand, normally fruit during the dry season. They produce large volumes of seeds, which are simultaneously dispersed on days with low relative humidities. For the same re-

Table 16.1. Seed species found by germination from soil samples taken in primary and secondary rain forest vegetation in Veracruz.[a]

Primary vegetation soil only	Both primary and secondary soils	Secondary vegetation soil only
Primary species	Secondary species	Primary species
Enterolobium cyclocarpum	*Ageratum conyzoides*	*Brosimum alicastrum*
Sapium lateriflorum	*Amaranthus hybridus*	*Lauraceae* spp.
Turpinia occidentalis	*Bidens pilosa*	
	Clibadium arboreum	Secondary species
Secondary species	*Eupatorium* spp.	*Clibadium grandifolium*
Axonopus compressus	*Eupatorium macrophyllum*	*Dioscorea* spp.
Belotia campbelli	*Heliocarpus* aff. *donnell-smithii*	*Emilia sonchifolia*
Cecropia obtusifolia		*Eupatorium pensamalense*
Costus spicatus	*Iresine celosia*	*Euphorbia heterophylla*
Croton draco	*Nuerolaena lobata*	*Heliocarpus appendiculatus*
Desmodium adscendens	*Panicum trichoides*	
Erechtites hieracifolia	*Piper umbellatum*	*Jacobinia* spp.
Eupatorium pycnocephalum	*Phytolacca rivinoides*	*Lasiacis papillosa*
Mirabilis jalapa	*Robinsonella mirandae*	*Mikania micrantha*
Pleuranthodendron mexicana	*Solanum cervantesii*	*Paspalum* spp.
Sida acuta	*Vernonia* aff. *deppeana*	*Physalis pubscens*
Trema micrantha		*Solanum nigrum*
		Solanum torvum
		Spigelia palmeri
		Urera caracasana
		Verbesina greenmani

[a] Data from Guevara and Gomez-Pompa (1972).

gion, this phenomenon has been observed for *Heliocarpus* spp. (Vazquez-Yanes 1976a) and for *Ochroma lagopus* (Garcia-Gutierrez 1976). This strategy leads such individuals to form a wide and uniform seed shadow. The pioneers most efficient in colonizing clearings and recently devegetated land undoubtedly produce uniform seed shadows over extensive areas; otherwise, it would be difficult to explain the presence of their seeds in soil of the mature rain forest after disturbance. The seed shadow (seed rain) of animal-dispersed species can be produced by efficient dispersal agents, for example, birds and bats, with a wide activity radius, which indiscriminately visit both disturbed and undisturbed areas (Trejo 1976; Vazquez-Yanes et al. 1975).

The most constant and abundant colonizing species of clearings and devegetated land combine wide dispersability, prolonged survival of viable seeds in the soil, and specialized mechanisms for triggering germination. One of the best-known species of this type is *Cecropia obtusifolia*, which produces seeds all year that are dispersed by numerous vectors, are abundant in the rain forest soil, and exhibit a prolonged photoblastic dormancy (Vazquez-Yanes 1979, 1980).

In comparison to the above, the majority of mature rain forest trees normally have large seeds with a high water content that tend to germinate rapidly after dissemination. This might be explained by the fact that seedlings of these species experience shady conditions during the initial moments of life. Therefore, they possess abundant food reserves, which allow them to achieve a certain size and form a large photosynthetic area in order to achieve a rate of net photosynthesis sufficient to maintain life. Rapid germination, moreover, creates seedlings, which due to their active metabolism and lower nutrient content, may be less susceptible to predation than the large and very conspicuous seeds.

We conclude that those seeds that tend to establish themselves in the continuous, stable, and shady rain forest habitat are large and have a short viability and brief dormancy. Species found in a discontinuous, unstable, sunny habitat, represented by clearings, have small seeds with long viability and specialized dormancy. In temperate and dry tropical forests, seeds of the mature vegetation normally have longer viability and specialized dormancy. In these cases, species are adapted to a climate with a long season, unfavorable for plant establishment, which the seeds must survive before they can germinate. Meanwhile, in the humid tropical rain forest, this unfavorable season is usually brief, or nonexistent in certain equatorial regions. Moreno-Casasola (1976) compared seed viability of rain forest and temperate forest species. In the first case, the majority of seeds are viable for only a few weeks, while in the latter, viability can last on the average of one or more years.

With respect to the mechanisms that trigger germination of pioneer species, these show, in general, exogenous dormancy or stress by unfavorable external factors. When these factors are removed, the seed population germinates simultaneously, thereby promoting rapid colonization. The most frequent type of dormancy is photoblastic, caused by an inadequate intensity or quality of light. This type occurs in important species, such as *Cecropia obtusifolia*, *Trema micrantha*, *T. guineensis*, and *Piper* spp. (Vazquez-Yanes 1976a,b, 1978, 1979). Integument dormancy occurs in *Ochroma lagopus*, *Heliocarpus appendiculatus*, and *H. donnell-smithii* (Vazquez-Yanes 1974, 1976a).

The quality of diffuse light within the rain forest inhibits germination due to its richness in far-red versus red light. Opening the canopy allows direct sunlight to enter, which changes the red-to-far-red ratio and triggers germination (Vazquez-Yanes 1976b).

With respect to the longevity of viable seeds in the soil, little information exists for the tropics. Juliano (1940) in the Philippines found that buried seeds of certain tropical weeds can remain viable for 7 years. Castro and Guevara (1976) observed that 21 species germinated from samples of soil stored in the laboratory for 1 year. Among the species that appeared were *Cecropia obtusifolia*, *Piper auritum*, and *Trema micrantha*. Lebron (1979) in Puerto Rico reported that seeds of *Palicourea riparia*, a rubiaceous shrub present in the mature rain forest, but more abundant in cut areas, can remain viable in the soil for at least 3 years.

The seed pool in the soil will generate mixtures of species with different floristic compositions, depending on the treatment received by the soil. One clear example of this is the work of Vazquez-Yanes (1974) on *Ochroma lagopus*. When soil samples were treated with heat similar to that of a forest fire, the number of species that subsequently germinated was less than in unheated soils. *Ochroma lagopus* dominated the seedlings in the treated soils, since the seeds of this species are resistant to high temperatures and are actually stimulated to germinate by heat (Table 16.2). At the same time, if seeds of rapidly growing weed invaders are abundant in a soil, their growth can affect the composition of the vegetation. In an experiment by Lopez-Quiles and Vazquez-Yanes (1976) examining soil samples with known quantities of weed species seeds, *Bidens pilosa* was so aggressive in its growth that it inhibited pioneer species such as *Ochroma lagopus* and *Cecropia obtusifolia*. Germination can generate interspecific competition among the components of the seed pool. This competition, modified by external factors, will ultimately determine the composition of the initial vegetation of a cleared site.

The Role of Pioneer Species in Regeneration

According to Whitmore's (1975) classification, rain forest species can be divided into four groups based on their responses to openings in the canopy. These are: (1) trees whose seedlings are established and grow

Table 16.2. Effect of heat on the composition and number of seedlings that appear in soil samples from a secondary forest of *Ochroma lagopus*.[a]

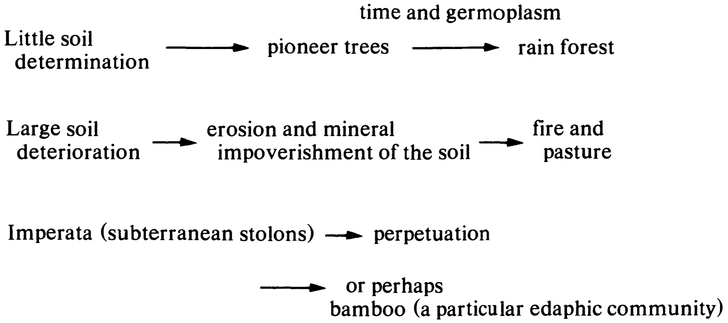
		Unheated soil				Dry heated soil (80°C)				Soil heated with boiling water			
Seedlings	Replicates	10	20	30	Total	10	20	30	Total	10	20	30	total
Ochroma	1	23	2	0	25	60	4	1	65	66	3	0	69
lagopus	2	3	3	0	6	23	1	0	24	30	0	0	30
Total:		26	5	0	31	83	5	1	89	96	3	0	99
Other	1	81	260	98	439	8	5	4	17	31	38	18	87
species	2	31	117	72	220	2	0	1	3	25	20	11	56
Total:		112	377	170	659	10	5	5	20	56	58	29	143
Number of	1	8	9	2	19	2	0	1	3	3	3	0	6
different species	2	5	4	1	10	2	0	0	2	2	0	1	3

under the intact canopy of the rain forest; (2) species that germinate and grow principally under the rain forest canopy, but appear to benefit from the existence of openings; (3) trees that establish themselves under the rain forest canopy but definitely need openings to grow; and (4) pioneer species that establish themselves principally in clearings and grow only in these openings, this group being divided into species with long or short life cycles. Pioneer, short-lived trees and shrubs, or "weed trees," which do not form part of the mature vegetation, grow rapidly, reaching sexual maturity in a few years, and have a short life span, in comparison to species of later seral stages. These species generate peculiar environmental conditions after becoming established, which inhibit their own replacement and allow the growth of species characteristic of later successional stages (Vazquez-Yanes 1980).

The abundance of pioneer trees and shrubs in a rain forest region depends on the frequency of openings in the canopy that allow direct sunlight to strike the forest floor for a large part of the day. In undisturbed primary rain forest areas, these species develop only in large clearings caused by tree falls. They can also be very abundant along river banks, on rocky soils, or on slopes, which experience more frequent tree falls because of overland water flow and winds. The vegetative cover of the rain forest is subject to relatively frequent alterations independent of human activity. Whitmore (1978) and Hartshorn (1978) calculated that tree falls that uncover the soil of the rain forest occur on the average of every 80–90 years. Small clearings are filled by species that existed in the site as seedlings before the disturbance, while large openings are colonized by rapidly growing pioneer nomads (Schulz, 1960). Kramer (1933) in Indonesia observed that clearings of 0.1 ha or less were promptly colonized by the surviving seedlings of the rain forest. However, in clearings of 0.2–0.3 ha or more, the growth of pioneer species prevented the growth of rain forest seedlings. Knight (1975), as part of a phytosociological study of Barro Colorado, Panama, noted that *Cecropia obtusifolia* was more abundant in the oldest and highest rain forest on the island than in the late secondary rain forest. This may be due to the fact that clearings, produced by tree falls, are much larger and more frequent in the former than in the latter. This suggests that a group of species with nomadic behavior, which forms typical cicatricial vegetation, evolved and diversified in rain forest clearings. The abundance of these species has grown enormously due to human activity, which probably also has favored genotypic and phenotypic variation in these species, as with other taxa characteristic of anthropogenic vegetation (Gomez-Pompa 1971). The most common pioneer trees of the world's tropics belong to the genera *Adinandra* spp. (Ternstroemiaceae), *Anthocephalus* spp. (Rubiaceae), *Cecropia* spp. (Moraceae), *Didymopanax* spp. (Araliaceae), *Harungana* spp. (Hypericaceae), *Heliocarpus* spp. (Tiliaceae), *Macaranga* spp., *Mallotus* spp. (Euphorbiaceae), *Musanga* spp. (Moraceae), *Ochroma* spp. (Bombacaceae), *Piper* spp. (Piperaceae), *Trema* spp. (Ulmaceae), etc.

The relationship between clearing size and establishment of pioneer species can be affected by nutrient availability in the soil. Plants of the mature rain forest have mycorrhizae (Singh 1966; Went and Evans 1968), while apparently many pioneer species lack mycorrhizae or do not require them to achieve rapid growth. This suggests that for a pioneer species to establish itself, the clearing must be large enough to allow the plant to exist as well as contain sufficient space for root colonization and proper conditions for mineralization of soil nutrients. In small clearings, the dense mat of roots and superficial mycorrhizae of the mature community is so closed that only seedlings with roots integrated into the mat can survive. In large clearings, the death and fall of some trees reduces root competition, thereby allowing the establishment of plants that obtain nutrients, at least initially, in the free ionic form.

Pioneer tree establishment is impeded or retarded in soils impoverished by cultivation or pasturing. In these soils, perennial grasses such as *Bambusa* spp., *Imperata* spp., and slow-growing sclerophyllic trees and shrubs such as *Guazuma* and *Curatella* become established. When this occurs, the successional process is retarded or interrupted, resulting in the persistence of anthropogenic vegetation for considerable periods of time, depending on the recurrence of disturbance. In some cases succession is arrested indefinitely if species of the mature vegetation from the area (Gomez-Pompa et al. 1972) are absent. This process was described according to the following diagram by Whitmore (1975) for Southeast Asia:



We have observed something similar to the above in southeastern Mexico, although the process has not been analyzed quantitatively.

The rapid growth of pioneer species is due primarily to an energetic investment, directed at forming new tissue for increasing the photosynthetic surface of the plant. This process has been described in some detail for *Trema* and *Musanga* by Coombe (1960) and by Coombe and Hadfield (1962); these authors conclude that the rapid growth of these species is not due merely to an increase in dry weight, which is characteristic of more slow-growing tree species, but to the continual and efficient development of new foliar surface in a climate constantly favorable for photosynthesis.

According to the studies of Lugo (1970), the photosynthetic saturation and compensation points of certain pioneer trees allow high net photosynthetic values under intense direct sunlight. Apparently, their photosynthetic apparatus is not adapted to low intensity and diffuse light. Meanwhile, mature rain forest species, though less efficient photosynthetically at high light intensities, are adapted to low light conditions. Therefore, the latter can take advantage of increased light intensity due to small openings in the canopy. Consequently, the same individual can have leaves functional in the sun or shade.

The rapid growth of pioneer trees is due overall to their peculiar architecture and the ways they utilize photosynthate in their structure. Their energetic investment in woody tissue is comparatively small. Consequently, these tissues are light and rich in cellulose, but little lignified. The wood is usually fragile, and susceptible to fungal and parasite attack when its growth is interrupted by competition with other trees for nutrients and light at the end of the life cycle.

Growth rate, measured by Aubreville (1947), Lebrum and Gilbert (1954), and Blum (1968), for various pioneer tree species can be as high as 2–3 m annually (Fig. 16.3). From studies of pioneer tree architecture, Ashton (1978) deduced that their growth form leads to the formation of parasol type canopies in trees occupying the highest strata in early secondary succession (growth type Rauh, according to Halle et al. 1978). However, those species that occupy lower height strata exhibit a different architecture. Thus, utilization of available light is optimized at each level.

The secondary rain forest composed of pioneer species affects the environment in three different ways, which are extremely important for the development of vegetation through succession. These are: (1) transference of free nutrients from the soil to the biotic community, thereby decreasing the likelihood of their loss from the ecosystem; (2) edaphic structure improvement through the production of a large quantity of organic matter; and (3) microclimate modification, which reduces thermal fluctuations and increases atmospheric relative humidity. These effects promote the establishment of late successional species that subsequently will replace the pioneer trees in the community.

Immobilization of nutrients occurs rapidly. Communities at 10 months old contained the same quantity of nutrients as a mature grass field (Tergas and Popenoe 1971). By 6 and 14 years, secondary rain forests dominated by *Cecropia obtusifolia* and *Musanga cecropioides*, respectively, had immobilized almost as much phosphorus as a 50-year-old rain forest (Bartholomew et al. 1953; Greenland and Kowal 1960; Golley et al. 1975) (Table 16.3). In addition, the levels of certain soluble ions in the soil may also increase. Kellman (1969) reported that soil in sites dominated by *Trema orientalis* in the Philippines contained 110 milliequivalents of assimilable phosphorus per 100 g of soil, or almost double the highest values obtained under the other types of vegetation studied.

In reference to litter production, Golley et al. (1975) in Panama and Ewel (1976) in Guatemala found that secondary rain forests, between 6 and 14 years old, dominated by *Cecropia*, produced as much litter as mature rain forests in the region. This is due to the rapid replacement of pioneer species leaves, which enrich the organic matter content of the

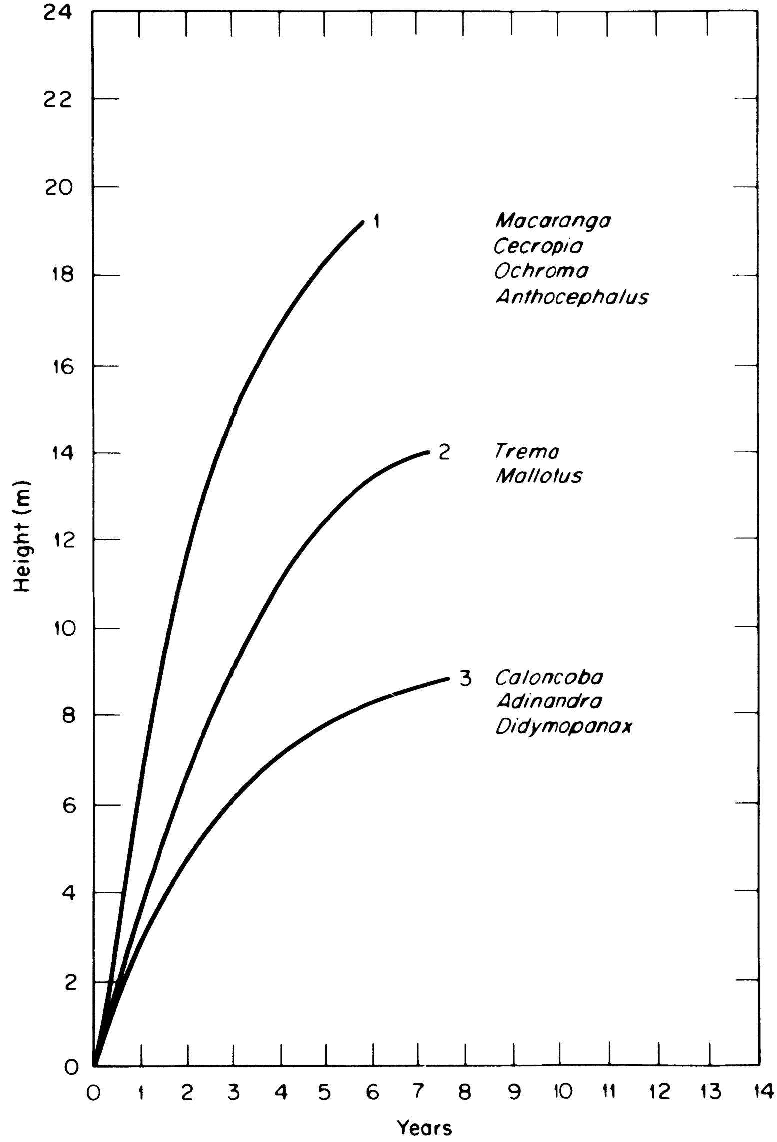


Figure 16.3. Growth rate among certain pioneer tree genera from the humid tropics.

Table 16.3. Nutrient content in primary and secondary vegetation from different places.[a]

Nutrient[a]	A	B	C	D	E	F	G	H
N	579	701	2061	—	—	—	—	—
P	35	108	137	85	241	72	154	163
K	839	601	906	1606	4598	524	1256	903

[a] A, B = 8- and 18-year-old secondary vegetation with Musanga in Zaire (Bartholomew et al. 1953); C = 80-year-old forest in Ghana (Greenland and Kowal 1960); D, E = two primary forests in Panama (Golley et al. 1975); F, G, H, = 2-, 4-, and 6-year-old secondary forest with Cecropia in Panama (Golley et al. 1975).

[b] Nutrient content in kg/ha.

soil. Ultimately, this enrichment facilitates the establishment and growth of seedlings with mycorrhizal roots from later seral stages, which obtain their nutrients, in part, from the decomposition of organic matter.

According to Golley et al. (1975) the structural characteristics of the vegetation change rapidly as the vegetation ages. The leaf area index of a 6-year-old rain forest, dominated by *Cecropia*, is almost the same as that of a mature rain forest, even though the average tree height and dbh of the 6-year-old forest were three times less. These data suggest that the productivity of the rain forest is rapidly reestablished, while the supporting structures, composed of stems and branches, develop slowly during succession. From 4 to 6 years, root biomass increases much faster than above-ground biomass, which explains in part the rate of nutrient immobilization (Table 16.4).

The characteristic microclimate of cleared land is modified in a short time by the establishment of trees. Ross (1954) and Snedaker (1970) measured temperature, relative humidity, and light in secondary rain

Table 16.4. Volume and biomass values for 2-, 4-, and 6-year-old tropical forests.[a]

	Age (yr)			
	2	4	6	Mature
Foliar surface (m^2/m^2)	8	12	17	11-22
Foliar volume (m^3/ha)	4	6	7	8-12
Total volume (m^3/ha)	16	42	57	276-338
Overground biomass (kg/ha)	13,020	38,040	42,550	
Underground biomass (kg/ha)	2600	4500	14,200	
Total biomass (kg/ha)	15,620	42,540	56,750	

[a] Foliar surface and volume and total above-ground volume is also given for mature forest.

forests of 5 and 14 years. Their results indicate that by year 14 microclimatic conditions are very similar to those of the mature rain forest. The environmental conditions caused by the growth of the pioneer tree community prevents their continued existence, and leads to their replacement by other species. Pioneer species, therefore, play a decisive role in regeneration and are a fundamental key to understanding this process. Their study can, undoubtedly, resolve many uncertainties that exist with respect to succession.

The chemical interactions between plants during succession undoubtedly can have some effect on vegetation development, since species with high allelopathic potential can affect the growth of other plants. In this respect, the work of Gliessman and Muller (1972) showed that phytotoxins of "bracken" fern (*Pteridium aquilinum*) can affect the establishment of other species. In our region, the work of Anaya and Anaya (1976) and Anaya and Rovalo (1976) indicates that certain typical secondary successional species of the genera *Piper* and *Croton* contain terpenes. When liberated into the environment, these compounds markedly affect the germination and growth of other species. However, these results were obtained under experimental laboratory conditions (Fig. 16.4). The demonstration of allelopathy in the tropical rain forest is extremely difficult under natural conditions. Nevertheless, the study of allelopathy is indispensible to understanding population dynamics, especially during the initial stages of regeneration.

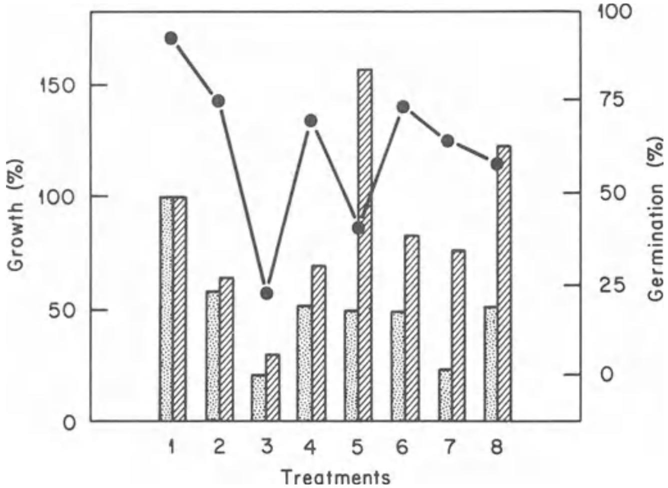


Figure 16.4. Effect of water extracts from secondary vegetation plants on the germination and seedling development of *Achyranthes aspera*. The treatments were: (1) pure water; (2) *Piper auritum*; (3) *P. hispidum*; (4) *Croton pyramidalis*; (5) *Cecropia obtusifolia*; (6) *Siparuna nicaraguensis*; (7) *Myriocarpa longipes*; (8) *Urera caracasana*. The hatched bars represent the seedlings shoots and the dotted bars the roots (taken from Anaya 1976).

Regeneration within the Rain Forest

One important fact to remember is that the primary rain forest is not a static community, but is in a process of continual change. Individuals in the herb and shrub layer die, other individuals appear, the epiphyte community is constantly changing, and some animals and microorganisms change seasonally. The rain forest trees, both juveniles as well as adults, grow in height and diameter. Some change their leaves seasonally; other replace foliage without apparent periodicity. The overall sensation of stability is due to the large trees, whose presence dominates in many senses, physiognomically as well as physiologically. Nevertheless, rain forests are in a dynamic process of change, which includes the slow substitution of the dominant tree species. In relation to this, Schulz (1960) says: "They are regenerating rather continuously and maintaining the existing proportions in the population."

If we examine a profile of the rain forest (Richards 1952), we will find dominant tree species, represented by individuals of different ages, living in lower height strata. This fact has been interpreted to mean that the primary community is stable and is regenerating. However, this is not totally correct. Only some species exhibit this pattern. Other species require another process for their regeneration, such as following obligate, sun-loving species (Whitmore 1975).

As part of the process of rain forest regeneration, we should also consider regeneration in old secondary or stable primary rain forests. We are therefore referring to the process of regeneration within a rain forest that is not prompted by a noticeable ecosystem disturbance. This process is actually more difficult to observe and perhaps of lesser importance than the process of tropical forest regeneration via secondary succession, which is probably more widespread in the tropics. However, if we assume that the process of internal rain forest regeneration under original conditions, especially before the appearance of humanity, was the precursor of the process of secondary succession, then understanding it can be essential for rain forest management.

If we visit a mature rain forest in a hot-humid region, we find it is relatively easy to walk on the forest floor, which is covered with litter and different-sized plants that are juveniles of many species found in the upper canopy. In some seasons, especially after fruiting, seedlings are extraordinarily abundant, covering the rain forest soil. However, in a few weeks or months the majority will die, and only a few will continue growing. These juvenile rain forest trees are so characteristic that we suppose they are enormously important to the process of internal rain forest regeneration. Studies in Los Tuxtlas (del Amo 1978) provided very interesting information on the behavior of primary tree seedlings and saplings with respect to the length of their growth (Table 16.5) and their enormous capacity to regenerate foliar tissue. These results suggest that

Table 16.5. Growth and leaf formation in seedlings of tropical rain forest trees under different natural light conditions.[a]

	Growth (cm/yr)			New leaves per year		
Species	S	A	CPS	S	A	CPS
Poulsenia armata Standi	2.83	2.55	17.04	2.55	—	—
Rheedia edulis (Seem) Triana & Planchon	1.35	4.14	11.75	4.81	4.74	12.15
Nectandra ambigens	2.73	3.24	33.94	N.S.	5.03	10.69
Licaria alata Miranda	3.32	ns	5.11	—	—	—
Chamaedora tepejilote Liebm.	1.05	2.44	11.16	2.55	1.752	2.92

[a] S, primary forest; A, 15-year,old secondary forest, CPS, cleared primary forest.

in these species there exists a very delicate physiological equilibrium between photosynthesis, growth of the individual, and the relation of growth to the root system. These individuals will continue growing, through time, if a severe disturbance, such as the fall of a close tree or large tree branch, does not occur. They become the regenerative potential of the species, living as shade-tolerant individuals in the lower strata of the rain forest. Seedlings of the same species in different environmental conditions, such as those under the shade of secondary species or in the direct sun, behave differently. This suggests that these species are preadapted to disturbance, since they can behave like sun-loving species before the opening of the canopy and as shade-tolerant species under secondary cicatricial trees. This interesting phenomenon is currently being studied and offers enormous opportunities for understanding the original regeneration process through species evolution. Natural selection acts on different stages of the life cycle of the species, selecting those characteristics that will be most competitive within the regeneration process under different environmental conditions. According to the calculations of del Amo (1978), *Poulsenia armata*, a primary rain forest species, reaches its height maximum in nondisturbed conditions at an age of 180 years. However, if a light gap appears, growth time to maximum height may be cut in more than half, to 70 years, if other tree species do not interrupt its growth through premature shading. In reality, the latter happens in a majority of large rain forest clearings, where the juveniles of the primary trees are overtopped by pioneer cicatricial species before they can increase their growth into the light gap. Investigators who have studied light gap regeneration (Hartshorn 1978; Whitmore 1978) observed that the rate of regeneration can vary, depending on many factors that occur in a site and/or distinct events that occur through time. Many of the secondary species are preadapted to severe changes in the environment, while the primary species that have a more predictable behavior and are more vulnerable, are not.

Conclusions

The most obvious conclusion to be derived from the present status of our knowledge of succession in tropical ecosystems is the enormous importance of understanding the life cycles of the species involved in the process of regeneration of the forest. These cycles can provide ways to investigate regenerative stages in time as well as space.

There exists an enormous diversity of tropical ecosystems in the world. Of these, only a few sites that are probably not comparable climatically or edaphically have been studied. Of the millions of species of plants and animals in the tropics, we know with some detail (although superficially) the life cycles of only a few. Until our knowledge increases, it will not be possible to arrive at a general concept of succession in the tropics.

Our only course is to continue along the same lines, to investigate more species in greater depth, and to broaden our investigations to include more aspects of the life cycles of the species. Only after the life cycles of the most important species are clearly understood, and, through this knowledge, an understanding of the interrelationships of the species is understood, will it be possible to investigate the succession of communities as a whole. Perhaps then we can ultimately discover the true nature of succession in the tropics.

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Index